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Maltodextrin acceptor reactions of *Streptococcus mutans* 6715 glucosyltransferases*

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ABSTRACT

The maltodextrin (maltose through maltoheptaose) acceptor reactions of two *Streptococcus mutans* 6715 glucosyltransferases (GTF-I and GTF-S) were studied. The acceptor product structures were determined by comparing them with the known structures of the acceptor products of *Leuconostoc mesenteroides* B-512FM dextransucrase (EC 2.4.1.5) and *L. mesenteroides* B-1355 alternansucrase (EC 2.4.1.140). When reacted with maltose (G2), both GTF-I and GTF-S transferred a D-glucopyranose from sucrose to the nonreducing glucosyl residue to give panose (6^2-α-D-glucopyranosyl maltose). Panose then served as an acceptor to give two further acceptor products, 6^2-α-isomaltosyl maltose and 6^2-α-nigerosyl maltose. 6^2-α-Isomaltosyl maltose then went on to serve as an acceptor to give a series of homologous acceptor products with isomaltodextrin chains attached to C-6 of the nonreducing-end residue of maltose, while 6^2-α-nigerosyl maltose did not further react. When reacted with other maltodextrins (G3–G7), both GTF-I and GTF-S transferred a D-glucopyranose to C-6 of either the nonreducing-end or the reducing-end residues of the maltodextrins, forming α(1→6) linkages. When D-glucopyranose was transferred to the nonreducing-end residue by GTF-I or GTF-S, the first product was also an acceptor to give the second product, which then served as an acceptor to give the third product, etc., to give a homologous series of products. When D-glucopyranose was transferred to the reducing-end residue, the acceptor product that formed did not readily serve as an acceptor, or served only as a very poor acceptor, to give a small amount of the next homologue, as was the case for G7 with GTF-S. In addition, GTF-I also transferred D-glucopyranose to the reducing-end or to the nonreducing-end residue of maltotriose, forming α(1→3) linkages, to give 3^3-α-D-glucopyranosyl maltotriose and 3^1-α-D-glucopyranosyl maltotriose. Neither of these acceptor products further served as acceptors to give a homologous series. Under equivalent conditions of equimolar amounts of acceptor and sucrose, maltose and maltotriose are much better acceptors with GTF-I than they are with GTF-S, which is better than *L. mesenteroides* B-512FM dextransucrase. The three enzymes display significantly different efficiencies for the different maltodextrin acceptor reactions, GTF-I and GTF-S having much higher efficiencies than *L. mesenteroides* B-512FM dextransucrase.

INTRODUCTION

Streptococcus mutans 6715 produces two D-glucans from sucrose, a water-soluble dextran containing 73% α(1→6) linkages and 27% α(1→3) branch linkages[1] and a

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water-insoluble glucan (a "mutan") containing 93% α(1→3) linkages and 7% α(1→6) linkages[2]. The enzymes that synthesize the soluble and insoluble glucans are usually referred to as GTF-S and GTF-I, respectively[3,4]. *S. mutans* has been shown to be the primary organism responsible for dental caries[5,6]. Its ability to form plaque on teeth surfaces is attributed to the production of these exocellular polysaccharides, which mediate cell–cell and cell–teeth adherence[5,6].

A mechanism for the synthesis of the glucans by *S. mutans* 6715 glucosyltransferases has been proposed[4] in which there are two catalytic groups on each enzyme that covalently links D-glucosyl and glucanosyl units. During the synthesis, the glucosyl and the glucanosyl units alternate between the two sites, giving elongation of the glucan by the addition of the D-glucosyl unit to the reducing end. When other carbohydrates, in addition to sucrose, are present in the digest, *S. mutans* 6715 glucosyltransferases also carry out acceptor reactions, in which D-glucopyranosyl units are transferred from the enzyme to the carbohydrates (acceptors) to form acceptor products[4,7,8].

When maltose serves as an acceptor, the acceptor products with both GTF-I and GTF-S were panose and a series of homologues of panose in which isomaltodextrin chains of varying lengths were linked to the nonreducing-end D-glucosyl residue of maltose by an α(1→6) linkage[7,8]. The structures of the acceptor products formed from other maltodextrins, such as maltotriose (G3) to maltoheptaose (G7), however, have not been determined. These acceptor products are important in that maltodextrins occur in the mouth from the action of salivary α-amylase on food starch. The resulting acceptor products of subsequent interactions of the maltodextrins with the glucosyltransferases from *S. mutans* could be contributing factors in the formation of dental plaque. Knowledge of their structures might be useful in the design of inhibitors or agents that could reduce, modify, or prevent dental plaque formation. We have, therefore, studied the acceptor reactions of *S. mutans* 6715 glucosyltransferases with maltodextrins (G2–G7).

EXPERIMENTAL

Carbohydrates and Reagents. — Maltodextrins, G3–G7, were a gift from Nihon Shokuhin Kako Co. (Japan). [U-^{14}C]Sucrose was purchased from Sigma Chemical Company (St. Louis, MO). All other chemicals were of reagent grade and commercially available.

Enzymes. — *S. mutans* 6715 glucosyltransferases (GTF-I and GTF-S) were prepared as previously described[4]. *L. mesenteroides* B-512FM dextransucrase (hereinafter designated as B-512FM) was purified from the culture supernatant through the stage of DEAE-cellulose column chromatography as previously reported[9]. Activities of the enzymes were determined by a radiochemical assay using [U-^{14}C]sucrose[9]. Assays of the GTF-I and GTF-S were conducted at pH 6.5 and 37°, and those of B-512FM were conducted at pH 5.2 and 25°. Enzyme activity is given in international units (IU), *i.e.*, μmoles of D-glucose incorporated into glucan per minute.

Acceptor reaction digests. — The GTF-I and GTF-S acceptor reaction digests (10

μL) contained 40mM [U-^{14}C]sucrose (1 μCi), 40mM acceptor maltodextrin, 20mM imidazole hydrogen chloride buffer (pH 6.5), 2mM calcium chloride, 0.02% sodium azide, and 50 mIU of GTF-I or GTF-S. B-512FM acceptor reaction digests contained 40mM [U-^{14}C]sucrose (1 μCi), 40mM acceptor maltodextrin, 20mM pyridine acetate buffer (pH 5.2), 2mM calcium chloride, 0.02% sodium azide, and 20 mIU of dextransucrase. The reactions were conducted for 12 h at 25°, at which point t.l.c. indicated that all of the sucrose had been consumed.

Separation of acceptor products. — Aliquots (5 μL) of the reaction digests were spotted onto a Whatman K5F t.l.c. plate (20 × 20 cm) for multiple ascending chromatography at 22° with four ascents of (a) ethylacetate–ethanol–water (2:2:1, v/v/v), or three ascents of (b) nitromethane–1-propanol–water (2:5:3, v/v/v). These two solvent systems were complimentary to each other in their separating properties: solvent (a) resolves the primary acceptor products (1a, 1b, etc.) of each maltodextrin acceptor reaction, and solvent (b) resolves the other homologous products (2b, 3b, etc.) for each of the maltodextrin acceptor reactions. Labeled products were located by autoradiog-

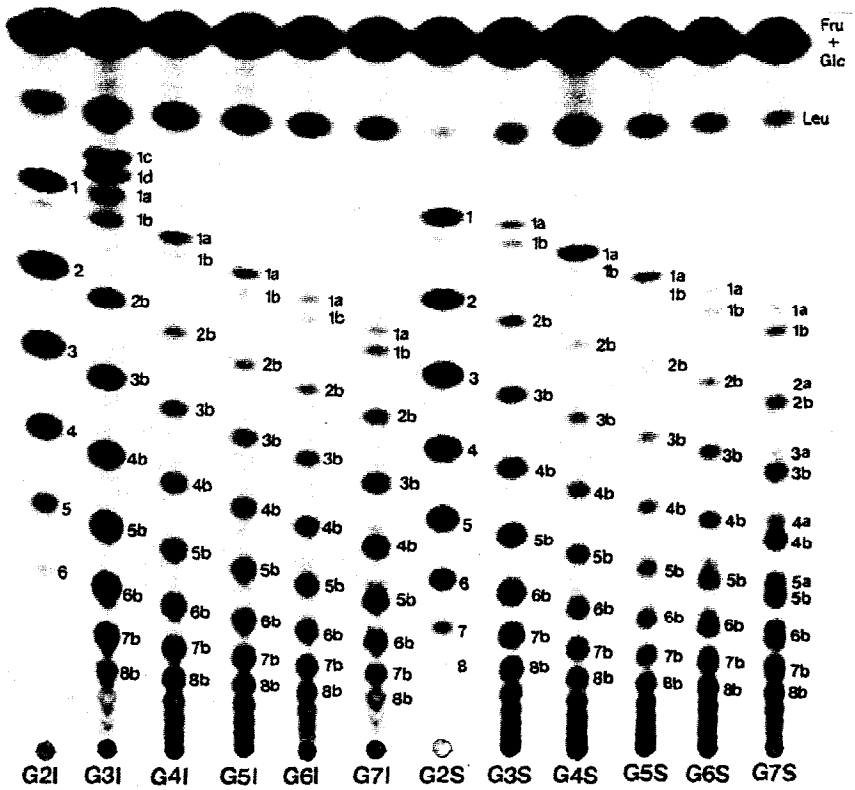

Fig. 1. Autoradiogram of a t.l.c. of the acceptor reactions of maltodextrins (G2–G7) with GTF-I (reactions G2I–G7I) and GTF-S (reactions G2S–G7S) where G2I is the maltose acceptor reaction with GTF-I, G3S is the maltotriose acceptor reaction with GTF-S, etc. Five μL of each acceptor reaction digest was spotted onto a Whatman K5F t.l.c. plate, which was developed with three ascents of nitromethane–1-propanol–water (2:5:3, v/v/v). Fru + Glc are D-fructose and D-glucose, and Leu is leucrose.

raphy. The quantitative analysis of the acceptor reactions were carried out by determining the radioactivities of the products on t.l.c. plates by using a Vanguard 2001 t.l.c. autoscanner.

RESULTS

All of the maltodextrins (G2–G7) in the presence of sucrose were D-glucopyranosyl acceptors for *S. mutans* 6715 glucosyltransferases, GTF-I and GTF-S (see Fig. 1). The acceptor reaction patterns shown in Fig. 1 were very similar to those of B-512FM, which gave panose as the first acceptor product from maltose. Panose was then an

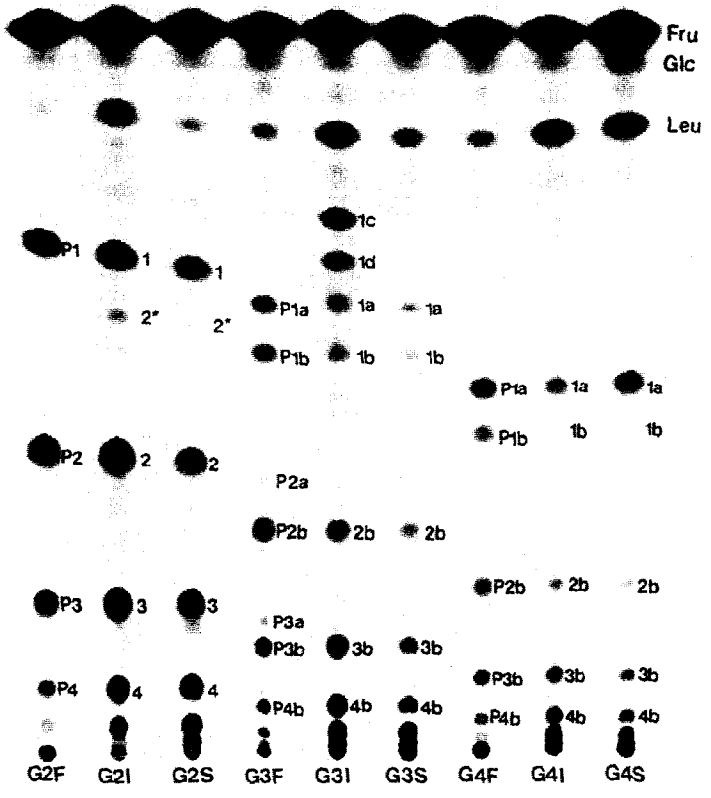

Fig. 2. Autoradiogram of a t.l.c. of the acceptor reactions of B-512FM dextransucrase, GTF-I and GTF-S with G2–G4, where G2F is the maltose acceptor reaction with B-512FM dextransucrase, G3I is the maltotriose acceptor reaction with GTF-I, G4S is the maltotetraose acceptor reaction with GTF-S, etc. Five μL of each acceptor reaction digest was spotted onto a Whatman K5F t.l.c. plate, which was developed with four ascents of ethyl acetate–ethanol–water (2:2:1, v/v/v). Fru, Glc, and Leu are D-fructose, D-glucose, and leucrose, respectively.

acceptor to give 6^2-isomaltosyl maltose† that was an acceptor to give 6^2-isomaltotriosyl maltose, etc., to give a homologous series of products with α-isomaltosyl-dextrin chains of varying lengths attached to C-6 of the nonreducing-end residue of maltose[11]. GTF-I and GTF-S each gave an essentially identical pattern with maltose (see reaction G2F, G2I, and G2S in Fig. 2). An exception was the formation of small amounts of a product labeled 2* and somewhat larger amounts of the acceptor products labeled 2, 3, and 4 in Fig. 2.

The minor product, labeled 2* in Fig. 2, has not previously been observed as an acceptor product for GTF-I and GTF-S. It, however, has been shown that the acceptor reaction of *L. mesenteroides* B-1355 alternansucrase with maltose gave panose as the first acceptor product[10]; panose then served as an acceptor to give two products, 6^2-α-isomaltosyl maltose and 6^2-α-nigerosyl maltose[10]. When t.l.c. of the maltose acceptor products of GTF-I and GTF-S were compared with the acceptor products of alternansucrase (see Fig. 3), it was observed that 2* migrated with 6^2-α-nigerosyl

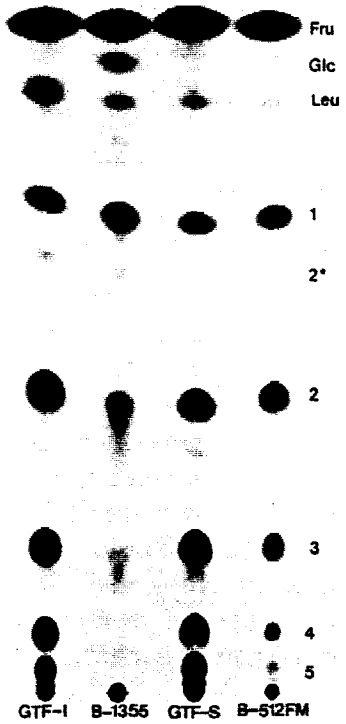

Fig. 3. Autoradiogram of a t.l.c. of the acceptor reactions of G2 with GTF-I, GTF-S, B-1355 alternansucrase and B-512FM dextransucrase. Five μL of each acceptor reaction digest was spotted onto a Whatman K5F t.l.c. plate and was developed with four ascents of ethyl acetate–ethanol–water (2:2:1, v/v/v). Fru, Glc, and Leu are D-fructose, D-glucose, and leucrose, respectively.

† Oligosaccharide nomenclature is that according to Whelan[12]. For example, 6^2-α-D-glucopyranosyl maltose is a trisaccharide with α-D-glucopyranosyl residue attached to C-6 of the second D-glucose residue of maltose. The large numeral is the carbon atom of attachment and the superscript numeral is the residue of attachment, with the reducing-end residue being no. 1.

maltose. The panose acceptor reaction of B-512FM does not give this product[11], and it appears to be formed by those glucansucrases that synthesize glucans with relatively high amounts of $\alpha(1\rightarrow3)$ linkages, such as GTF-I, GTF-S, and alternansucrase.

B-512FM gave two tetrasaccharide products with G3, P1a, and P1b, which had D-glucose attached to C-6 of the reducing-end residue and to the nonreducing-end residue[11], respectively (see reaction G3F in Fig. 2). One of these, P1b, went on to give appreciable amounts of a series of homologous products, P2b–P4b, while the other one, P1a, only gave a small amount of homologous products, P2a and P3a (see reaction G3F in Fig. 2). The major products from the reaction of GTF-S with G3 were identical to the major products produced by B-512FM (compare G3F with G3S in Fig. 2). There are, however, relative quantitative differences in the amounts of the products, with GTF-S giving lower amounts of P1a and P1b and higher amounts of P4b, P5b, P6b, etc. than B-512FM (see G3S in Figs. 1 and 2). B-512FM also produces small amounts of P2a, P3a, and P4a that GTF-S does not produce.

Reaction of GTF-I with G3, however, gave four tetrasaccharide products, 1a–1d of G3I in Fig. 2. One of these, 1b, was the same as 1b and P1b produced by GTF-S and B-512FM, respectively, and gave rise to the same homologous series as GTF-S and B-512FM (compare G3I with G3F and G3S in Fig. 2). Of the four tetrasaccharide products produced by the reaction of G3 with GTF-I, 1b was 6^3-α-D-glucopyranosyl maltotriose and 1a was 6^1-α-D-glucopyranosyl maltotriose, the same tetrasaccharide products produced by reaction of G3 with GTF-I and B-512FM. The position of chromatographic migration of 1c and 1d, suggests that they have the D-glucose attached to G3 by an $\alpha(1\rightarrow3)$ linkage. Oligosaccharides with $\alpha(1\rightarrow3)$ linkages generally migrate faster on chromatography than saccharides of comparable d.p. with $\alpha(1\rightarrow6)$ linkages in the same positions. Further, a D-glucose residue attached to the reducing-end residue moves faster than one attached to the nonreducing-end residue (compare the migration and structures of P1a and P1b for any of the maltodextrin acceptor reacting with B-512FM (Fig. 2 and ref. 11). In addition, because GTF-I also produces a glucan primarily with $\alpha(1\rightarrow3)$ linkages, it is most probable that the linkage for the attachment of D-glucose to G3 in products 1c and 1d would be an $\alpha(1\rightarrow3)$ linkage to the reducing-end residue for 1c and to the nonreducing-end residue for 1d. The proposed structures for 1c and 1d, therefore, would be 3^1-α-D-glucopyranosyl maltotriose and 3^3-α-D-glucopyranosyl maltotriose, respectively. The proposed structures of the four tetrasaccharide acceptor products of the reaction of GTF-I with G3 are summarized in Table I.

Reaction of G4 gave identical acceptor reaction patterns for the three enzymes (compare reactions G4F, G4I, and G4S in Fig. 2). The first products, P1a and P1b, have D-glucose attached to C-6 of the reducing-end residue and to the nonreducing-end residue, respectively, of the maltodextrin acceptors[11]. The P1b product was an acceptor to give a homologous series. The acceptor reactions with G5, G6, and G7 followed the same pattern, giving two primary products, P1a and P1b, of which P1b went on to give a homologous series and P1a did not. The acceptor product patterns for GTF-I and GTF-S reacting with G5–G7 (see Fig. 1) were the same as those produced by B-512FM[11]

TABLE I

Summary of the acceptor product structures of GTF-I and GTF-S with maltodextrins G2 to G7

Acceptor Reactions[b]	*Acceptor Products*[a]						
	1a	*1b*	*1c*	*1d*	*2**	*2b*	*nb*
G2I		6^2-α-Glc-G2			6^2-α-Nig-G2	6^2-α-Im-G2	6^2-α-$(Im)_n$-G2
G3I	6^1-α-Glc-G3	6^3-α-Glc-G3	3^1-α-Glc-G3	3^3-α-Glc-G3		6^3-α-Im-G3	6^3-α-$(Im)_n$-G3
G4I	6^1-α-Glc-G4	6^4-α-Glc-G4				6^4-α-Im-G4	6^4-α-$(Im)_n$-G4
G5I	6^1-α-Glc-G5	6^5-α-Glc-G5				6^5-α-Im-G5	6^5-α-$(Im)_n$-G5
G6I	6^1-α-Glc-G6	6^6-α-Glc-G6				6^6-α-Im-G6	6^6-α-$(Im)_n$-G6
G7I	6^1-α-Glc-G7	6^7-α-Glc-G7				6^7-α-Im-G7	6^7-α-$(Im)_n$-G7
G2S		6^2-α-Glc-G2			6^2-α-Nig-G2	6^2-α-Im-G2	6^2-α-$(Im)_n$-G2
G3S	6^1-α-Glc-G3	6^3-α-Glc-G3				6^3-α-Im-G3	6^3-α-$(Im)_n$-G3
G4S	6^1-α-Glc-G4	6^4-α-Glc-G4				6^4-α-Im-G4	6^4-α-$(Im)_n$-G4
G5S	6^1-α-Glc-G5	6^5-α-Glc-G5				6^5-α-Im-G5	6^5-α-$(Im)_n$-G5
G6S	6^1-α-Glc-G6	6^6-α-Glc-G6				6^6-α-Im-G6	6^6-α-$(Im)_n$-G6
G7S	6^1-α-Glc-G7	6^7-α-Glc-G7				6^7-α-Im-G7	6^7-α-$(Im)_n$-G7

[a] Abbreviations include the following: Glc, D-glucopyranose; Nig, nigerose; G2–G7, maltose–maltoheptaose; Im, isomaltose; and $(Im)_n$, isomaltodextrins with n = number of D-glucose residues. Oligosaccharide nomenclature is according to Whelan[12]. [b] G2I–G7I and G2S–G7S represent acceptor reactions of GTF-I and GTF-S with maltodextrins G2–G7.

TABLE II

Percentage of D-glucose from sucrose in GTF-I and GTF-S acceptor products with maltodextrins

Acceptor Reactions[b]	*Acceptor Products*[a]										*Dextran and higher d.p. products*	*% Relative Efficiency*[c]
	1a	*1b*	*1c*	*1d*	*2b*	*3b*	*4b*	*5b*	*6b*	*Leu*		
G2I		19.4			29.5	19.4	12.4	4.8	1.6	10.0	2.9	100
G3I	4.5	3.8	10.8	7.6	10.0	11.5	13.5	10.6	7.0	14.2	6.3	79.3
G4I	6.2	1.6			2.7	4.3	5.5	7.3		24.7	47.3	27.6
G5I	3.1	1.5			2.1	4.3	5.5	7.3		20.4	55.7	23.8
G6I	1.9	1.7			2.3	4.5	5.8	7.9		16.6	57.1	24.1
G7I	1.6	3.7			4.7	6.1	10.3			17.0	52.6	26.4
G2S		11.9			15.8	16.3	19.9	14.7	8.9	3.9	6.7	100
G3S	3.6	2.1			4.2	6.2	9.1	11.5		6.9	56.5	36.7
G4S	4.2	0.9			1.3	1.6	1.5	1.7		11.4	77.4	11.2
G5S	2.5	0.8			0.6	1.2	1.3	1.6		11.9	79.7	8.0
G6S	0.9	1.1			1.5	2.6	3.3	4.6		10.4	75.6	14.0
G7S	0.8	2.6			3.6	6.0	7.7			6.2	70.6	20.7

[a] Products of G2I and G2S are designated as 1b through 6b in Table II. [b] G2I–G7I and G2S–G7S represent acceptor reactions of GTF-I and GTF-S with maltodextrins G2–G7. [c] The relative efficiency of the acceptors was determined by comparing the amount of D-glucose from sucrose that was incorporated into acceptor products (exclusive of leucrose), assigning 100% efficiency to maltose.

(data not shown). The structures of the acceptor products of GTF-I and GTF-S with G5–G7 were thus deduced from the known structures formed by B-512FM[11] and are summarized in Table I.

A quantitative difference in the amounts of the higher saccharide products does occur at equilibrium (360 conversion periods for B-512FM and 900 conversion periods for GTF-S and GTF-I) for the three enzymes. GTF-I and GTF-S give more of the higher saccharide products (P4b and higher) and much less P1b than does B-512FM (See Fig. 2). They also give greater amounts of leucrose by reaction with D-fructopyranose than does B-512FM (Table II and ref. 13).

The distribution of the products at equilibrium and the relative efficiencies of the individual acceptor reactions are given in Table II. Table II shows that both maltose and maltotriose are much better acceptors with GTF-I than they are with GTF-S, which in turn is much better than B-512FM. Under equivalent conditions of equimolar amounts of acceptor and sucrose, maltose allows only 2.9% glucan to be synthesized by GTF-I, 6.7% glucan by GTF-S, and 28.4% glucan by B-512FM. The three enzymes thus have significantly different efficiencies for the acceptor reactions with maltose and maltotriose. Other quantitative observations are (*i*) that in the reaction with GTF-I, the efficiency of G7 (26.4%) is higher than the efficiency of G5 (23.8%) and G6 (24.1%), and (*ii*) that in the reaction with GTF-S, the efficiencies of G6 (14%) and G7 (20.7%) are higher than the efficiencies of G4 (11.2%) and G5 (8%). The method of analysis of the radioactivity on the t.l.c. by the autoscanner is reliable to $\pm 0.5\%$. The important point in these differences is that both GTF-I and GTF-S have a minimum efficiency when reacting with G5, and then both go up in efficiency in reacting with G6 and G7. The reaction of GTF-I with G7 goes up to 26.4% from a low of 23.8% for the reaction with G5, and the reaction of GTF-S with G7 goes up to 20.7% from a low of 8.0% for the reaction with G5. While the former is not as dramatic as the latter, the same trend is present, and the former has an overall higher percent efficiency for reaction with G7 than the latter. This is in contrast with the efficiencies of the maltodextrin acceptor reactions of B-512FM where they steadily drop as the size of the maltodextrin chain increases, with G7 having an efficiency of only 9.4% and G8 only 6.2% (ref. 11).

DISCUSSION

We have studied the maltodextrin (G2–G7) acceptor reactions of *S. mutans* 6715 glucosyltransferases, GTF-I and GTF-S. The structures of the maltodextrin acceptor products for GTF-I and GTF-S were very similar to those produced by B-512FM. Reaction with maltose, both enzymes gave panose as the first acceptor product, which went on to serve as an acceptor to eventually give a homologous series of 6^2-α-isomaltodextrinosyl maltose. It was also found that panose served as an acceptor for GTF-I and GTF-S to give two tetrasaccharides, 6^2-α-isomaltosyl maltose and 6^2-α-nigerosyl maltose. The latter product was relatively minor but was not formed by B-512FM. This might be expected as both GTF-I and GTF-S synthesize glucans with significantly higher percentage of $\alpha(1\rightarrow3)$ linkages than does B-512FM.

With G3, GTF-I gave different products than did GTF-S and B-512FM. The first products formed by GTF-I were four tetrasaccharides. Two of the tetrasaccharides have a D-glucose residue attached by an $\alpha(1\rightarrow6)$ linkage to the reducing-end residue of G3 and to the nonreducing-end residue of G3, and the other two have a D-glucose residue attached by an $\alpha(1\rightarrow3)$ linkage to the reducing-end residue and to the nonreducing-end residue of G3. GTF-S and B-512FM also gave the first two tetrasaccharide products but not the last two. All three of these enzymes elongated one of the tetrasaccharides (6^3-α-D-glucopyranosyl maltotriose) with the D-glucose attached by an $\alpha(1\rightarrow6)$ linkage to the nonreducing-end residue, to give a series of homologous products with isomaltodextrin chains of varying lengths attached by an $\alpha(1\rightarrow6)$ linkage to the nonreducing-end residue of G3. This is somewhat surprising for GTF-I in that the primary linkage in its synthesis of glucan is the $\alpha(1\rightarrow3)$ linkage, yet when GTF-I reacts with the maltodextrin acceptors that have one $\alpha(1\rightarrow6)$ linkage at the nonreducing-end, it gives the transfer of the D-glucose to C-6 of that nonreducing-end residue, forming an $\alpha(1\rightarrow6)$ linkage. This is further evidence that the elongation mechanism[4] of glucan synthesis is distinct from the glucosyl transfer reactions observed in the formation of acceptor products.

Reaction of G4–G7 with GTF-I and GTF-S gave the same product patterns that B-512FM gave. Two primary products were formed from each acceptor by the addition of D-glucose to C-6 of the reducing-end residue and to C-6 of the nonreducing-end residue of the acceptor. The latter product then served as an acceptor to give a homologous series of products, and the former product was not an acceptor or was a very poor acceptor. This difference in the ability of the initial acceptor products, P1a and P1b, to further serve as acceptors probably results from differences in their conformational and configurational structure, P1b being able to productively bind at the acceptor site and P1a not being able to productively bind.

There are several quantitative differences in the maltodextrin acceptor reactions of GTF-I, GTF-S, and B-512FM. GTF-I and GTF-S produced larger amounts of homologous series of products than did B-512FM. For B-512FM, the amount of homologous products decreased exponentially as the d.p. of the products increased, and acceptor products with d.p. >8 were not observed[11]. The maltose and maltotriose acceptor reactions of GTF-I were more efficient than GTF-S, which in turn was significantly more efficient than B-512FM. In addition, the efficiencies of the acceptor reactions for both GTF-I and GTF-S increased significantly after reaching a minimum with G5. Both GTF-I and GTF-S catalyzed the formation of greater amounts of leucrose than did B-512FM. The most efficient enzyme for the catalysis of all of the maltodextrin acceptor reactions was GTF-I.

Maltodextrins, especially G2 and G3, are produced in the oral cavity by the action of salivary α-amylase on food starch. These maltodextrins can then interact with food sucrose and GTF-I and GTF-S, produced by *Streptococcus* in the oral cavity, to form the products determined in this study. These products in turn can contribute to dental plaque formation. Thus, qualitative and quantitative knowledge of these reactions are important in the understanding of the mechanism of these enzymes and in the understanding of the formation and possible prevention of dental plaque.

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